

THE FLORAL MORPHOLOGY OF SOME SOUTH AFRICAN MEMBERS OF POLYGALACEAE.

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INTRODUCTION.

The family Polygalaceae is well represented in the temperate zone of southern Africa, three of the genera being common constituents of the Cape flora. Of these *Polygala* has a wide distribution over most of the world while *Muraltia* and *Mundia* are endemic to South Africa. While engaged on a taxonomic survey of the South African Polygalaceae the writer was impressed by the fact that certain species belonging to *Psilocladus*, a sub-genus of *Muraltia*,⁽⁵⁾ approached *Polygala* closely. Recently this fact has been emphasised by the discovery made by Miss E. Esterhuysen of a new species growing on high mountains in the western Cape Province. This species, which the writer proposes to name *Muraltia esterhuysenae* in honour of its discoverer, resembles *Polygala* in its large inner sepals, in the subdivided crest on the keel and in its fruit. In fact it is so similar to *Polygala*, that when first discovered it was regarded as a new species of that genus. Research, however, has shown that despite its close approach to *Polygala* in external form of the flower and fruit it is nevertheless a true *Muraltia*. The results given in this paper make that quite clear. Furthermore a comparative study of the species of the sub-genus *Psilocladus* has shown that the new species is closely allied to *Muraltia crassifolia*, another species characteristic of high mountains in the western Cape Province. In separating *Polygala* from *Muraltia* the surest means of diagnosis lies in the stamens. *Muraltia* always has seven stamens whereas *Polygala* has eight. In *Muraltia* the filaments are united almost to the base of the anthers, whereas in *Polygala* they are free for a considerable distance. Lastly the anthers in *Muraltia* dehisce by a longitudinal slit while in *Polygala* dehiscence takes place through a large, oblique pore.

In the past *Muraltia* has frequently been credited with eight stamens and it is a matter of historical interest to discover how this mistake first arose. When in 1737 Linnaeus established the genus *Heisteria* for the species we now know as *Muraltia heisteria*, he stated quite correctly that it had seven stamens.⁽⁶⁾ Shortly afterwards he must have felt uneasy about the rather unusual number seven for a few months later he described the same species in *Hortus Cliffortianus*⁽⁹⁾ and corrected his

earlier statement, saying that the number of stamens was usually eight but might occasionally be seven. Here we see the birth of a mistake which has persisted up to the present day. Evidently the number seven was so abnormal that its existence in a flower was regarded as highly improbable. Bergius when he described two species in 1767, erroneously attributed six stamens to one and eight to the other.⁽²⁾ De Candolle⁽⁴⁾ leaves the number of stamens an open question for under *Muraltia* the number of stamens is not mentioned. However by implication the number may be assumed to be eight for this was given as the number in the family as a whole and he did not alter it in the case of *Muraltia*. Harvey in the *Flora Capensis*⁽⁵⁾, Bentham and Hooker in the *Genera Plantarum*⁽¹⁾ and Phillips in the *Genera of South African Plants*⁽³⁾ all perpetuated the mistake made by Linnaeus in the 18th century. Marloth⁽¹¹⁾, whose statements were usually based on personal knowledge, stated the number to be mostly seven. In this he was followed in 1929 by the present writer⁽⁶⁾ who felt that although all the species growing on the Cape Peninsula and examined by her had seven stamens, there must be some foundation for the number eight so unequivocally given by eminent authorities in the past. Thus the possibility of *Muraltia* having eight stamens in certain cases was allowed to linger on. Now having examined nearly all the species of *Muraltia*, it is possible to say with certainty that the number is always seven. The probability that the number is never more than seven is borne out by a study of the floral morphology, the results of which are given below.

The following species have been investigated: *Polygala myrtifolia*, *Polygala virgata*, *Muraltia heisteria*, *Muraltia saxicola*, *Muraltia trinervia*, *Muraltia flanaganii*, *Muraltia esterhuysenae* and *Mundia spinosa*.

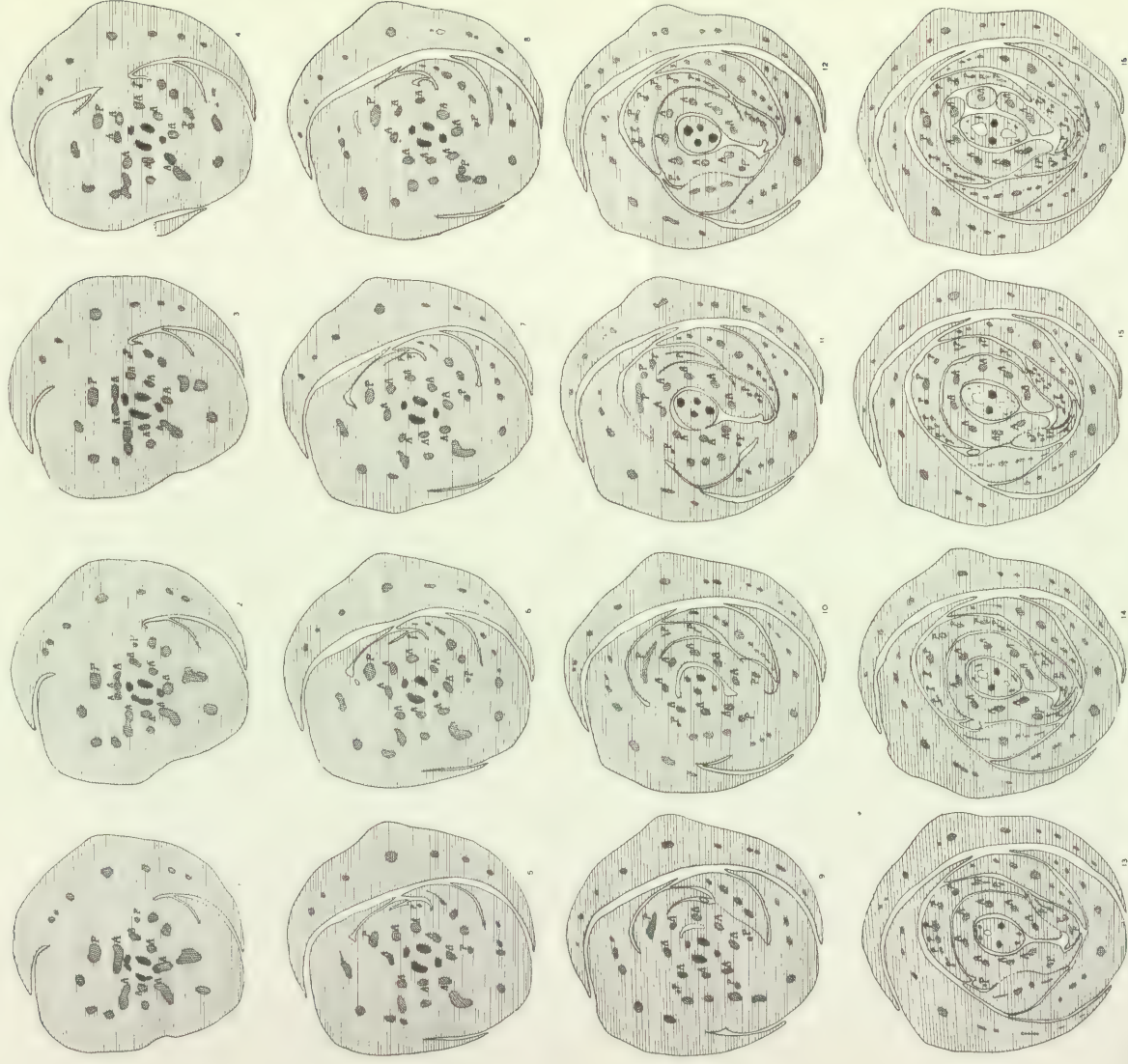
METHODS.

In all but *Muraltia esterhuysenae*, living flower buds were fixed in formalin-acetic-alcohol. In *Muraltia esterhuysenae* no fresh material was available, but in view of its importance dried flower buds were placed in boiling water until expanded and were then transferred to 70 per cent. alcohol. In all cases the buds were embedded in paraffin wax and serial sections cut, 12 μ in thickness. The sections were stained in Safranin and Fast Green.

All diagrams were made with the aid of a Leitz Panphot, the outlines, of the floral parts and their vascular strands being shown.

POLYGALA.

The structure of the flower in *Polygala* has been studied by several workers. Payer⁽¹²⁾ showed that in very young flower buds of *P. speciosa*



FIGS. 1—16. *Polygala nigrifolia*. Sections from the lower part of a flower bud. Vascular bundles are indicated by the more deeply shaded areas. Those which supply the gynoceum are shown in black, while the remainder are cross-hatched. Those marked "A" supply the stamens. Those marked "p" supply the petals. The vascular bundles of the sepals are not lettered.

there were rudiments of five petals but that the two median lateral petals aborted at an early stage so that in the adult flower only three petals were evident. He also pointed out that in the outer whorl of stamens the stamen opposite the posterior sepal was missing, while in the inner whorl that opposite the keel did not develop.

These findings were supported later by Chodat⁽³⁾ who stated that in most species the lateral petals remained rudimentary but that in *P. subuniflora* they were well developed and petaloid. He also mentioned that on rare occasions the missing stamens might develop.

The results obtained by the writer confirm those of the earlier workers who based their conclusions on developmental studies of very young flower buds in which the rudiments of the various floral parts were observed. In the present research a different method has been employed. Series of sections were cut through flower buds and by studying consecutive sections from the base of the flower upwards, it has been possible to determine the true floral nature of each part.

Polygala myrtifolia, on which the following account is based, was one of the species used by Chodat in his investigations. The writer has nothing essential to add to the account already given by Chodat⁽³⁾ but for comparison with *Muraltia*, diagrams are given drawn from sections through the lower part of the flower bud showing the origin of the various floral parts and their vascular strands. The sections were cut at a slightly oblique angle to the longitudinal axis of the flower, consequently the organs on the right-hand side of the diagrams appear earlier in the sequence than those on the left. However, making allowance for this, the origin of all the parts is clearly shown. In Fig. 1 only two petal traces are evident. The upper and larger one supplies the keel. The other belongs to one of the lateral petals which abort. In this section a large vascular strand, destined to supply two of the stamens, lies immediately within the strand supplying the keel. Fig. 2, drawn from a section 24μ higher up, shows the triple nature of the strand which therefore appears to be the potential vascular supply for three stamens. However, this appearance is lost almost immediately and two sections further on in the series (Fig. 3) two strands only are seen, just touching one another. Thus it is clear that the anterior stamen never develops and a very brief indication of its existence is all that is vouchsafed. In *P. myrtifolia* there is no indication at all of the posterior stamen. Fig. 4 shows the eight vascular strands belonging to the stamens, arranged in a ring round the strands of the gynoecium. These strands may be traced through all the succeeding figures until in Fig. 16 the initiation of the separation of the individual filaments is seen. The vascular strand supplying the keel

is apparent at a very early stage, but that belonging to the upper side petal becomes detached somewhat later. In Fig. 4 the latter may be seen, having just separated from one of the sepal traces. In this diagram the trace belonging to the abortive lateral petal is still visible and may be followed in Figs. 5, 6 and 7 as it passes into a small bulge which represents the rudimentary petal. In Figs. 8 and 9 the upper part of the petal may be seen after the disappearance of the vascular strand. A comparison of Figs. 4—14 will show the gradual separation of the lower right-hand petal from the staminal tube to which in its earliest stages it is completely united.

Similar behaviour of the various vascular strands on the left-hand side of the flower bud may be followed in Figs. 8—15.

Polygala virgata is similar to *Polygala myrtifolia* in its essential features but a few differences may be observed. Rudimentary side petals are not developed though their vascular strands are clearly seen, arising just as in *Polygala myrtifolia* opposite a stamen of the inner whorl. In an abnormal flower bud which had only seven stamens, the missing stamen belongs to the inner whorl and is one normally lying immediately within a rudimentary petal. In spite of the fact that both the stamen and its vascular strand are missing, the trace belonging to the obsolete side petal is developed in the usual way.

Polygala virgata shows no evidence of any vascular supply to the stamen opposite the keel such as has been demonstrated for *Polygala myrtifolia*. However, here a well-defined patch of phloem lying opposite the posterior sepal, is clearly visible close to the base of the flower. It persists for only a short distance but its presence in this position suggests that it is a relic of a posterior stamen, a stamen which rarely develops in the family. A stamen in this position has been recorded by Chodat in an exceptional flower in another species.

A study of the vascular anatomy of the flower confirms Chodat's view that the flower of *Polygala* is essentially pentamerous and that the common numbers, three for the petals and eight for the stamens, have arisen by reduction.

MURALTIA.

Little work has been done on the floral structure of *Muraltia* but Chodat, in the course of his monumental researches on the Polygalaceae, examined very young flower buds in two species. He found that *Muraltia* was quite different from *Polygala*. He could find no evidence that side petals had ever existed in the genus. He also pointed out that abortion in the androeceum had proceeded along different lines from that in *Polygala*. He concluded that of the three missing stamens, one was the



Figs. 17—31. *Muraltia flanaganii*. Sections of a flower bud, starting at the base and reaching the level of the anthers. The shading and symbols are the same as in *Polygala myrsifolia*.

posterior as in *Polygala* and the other two were those which should arise opposite the upper petals. This latter conclusion, as will be seen, is not supported by the present investigation.

On taxonomic grounds the sub-genus *Psilocladus* is regarded as more primitive than the other sub-genus, *Eumuraltia*. During the early part of the investigation two species were studied: *Muraltia trinervia* (*Psilocladus*) and *Muraltia heisteria* (*Eumuraltia*). The floral morphology proved to be similar in both, there being no significant differences between them. The writer felt that if the genus had retained any primitive features, they would be found in some species of *Psilocladus* inhabiting the mountains. In a previous publication(?) the writer brought forward evidence to show that the mountains have provided sanctuary for the Cape flora at times in its past history when arid conditions threatened its existence. If this has been so then obviously the more primitive members are to be sought in these sanctuaries. Miss E. Esterhuysen who is a keen mountaineer as well as a botanist, kindly offered to obtain material from high altitudes and three of these alpine species have now been included in the investigation: *M. saxicola* (*Eumuraltia*), *M. flanaganii* (*Psilocladus*) and *M. esterhuysenae* (*Psilocladus*). *M. saxicola* and *M. flanaganii* come from the upper slopes of the Drakensberg in Natal and *M. esterhuysenae* from mountains in the western Cape Province. Of all the species studied the only one which was in any way unusual was *M. esterhuysenae*. In the following account *M. flanaganii* is taken as a typical example of the genus.

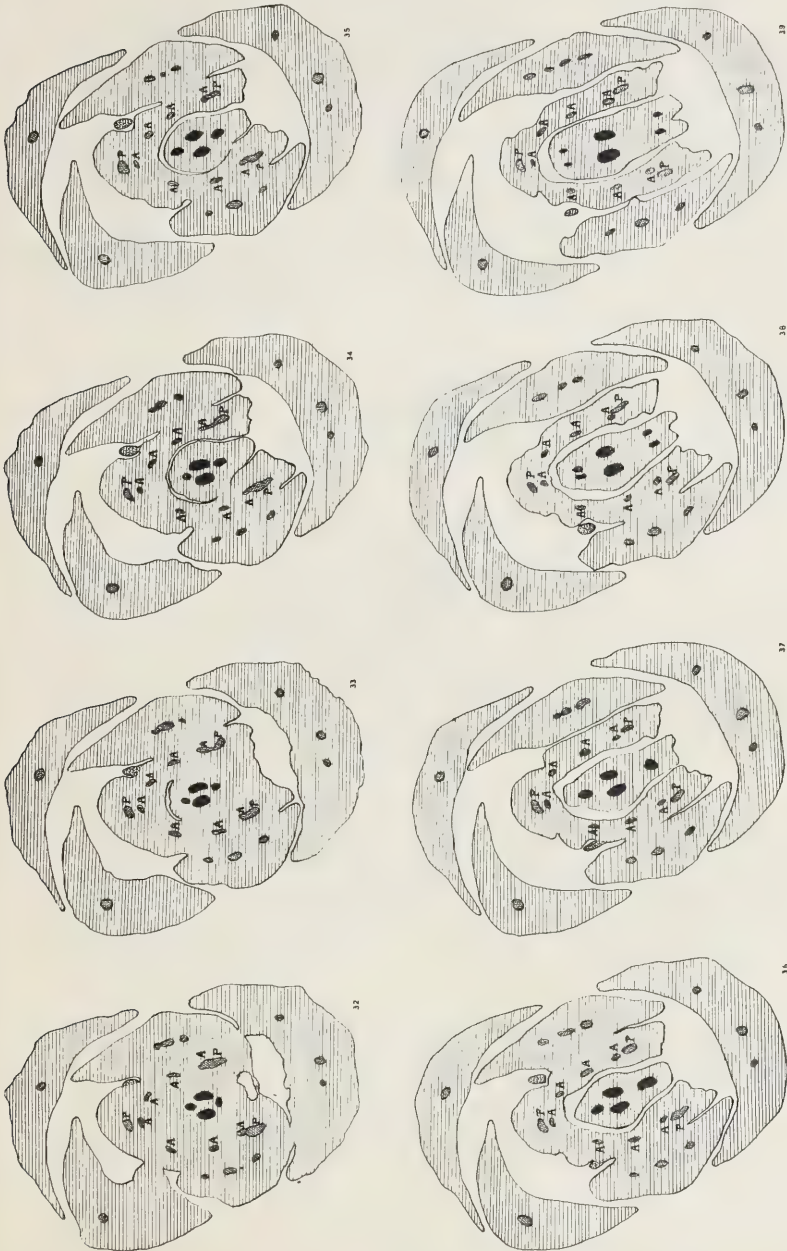
Fig. 17 is a section through the base of a flower when the vascular strands supplying all the floral parts are sharply differentiated. It will be noticed that even at this early stage the strands supplying the keel and the upper petals are clearly visible. The late development of the upper petals as seen in *Polygala*, is not a characteristic of *Muraltia*. The vascular strands supplying the stamens are clear and definite, and it is quite obvious that traces passing out into the two upper petals lie immediately outside the traces belonging to the two uppermost stamens. Thus Chodat was wrong in his supposition that two of the abortive stamens in *Muraltia* are those lying opposite the upper petals. Fig. 18 shows a section cut at a slightly higher level when the gynoeceum has separated from the tissue shaped like a horse-shoe and representing the fused stamens and petals. The section shown in Fig. 19 passes through the lower part of the ovary and shows differentiation of the upper petals. The next section (Fig. 20) is a little higher up, passing through the upper part of the ovary, and shows a slight increase in size of the side petals. In Fig. 21 the section passes through the four horn-like outgrowths on

the top of the ovary, with the style passing up between them. In Fig. 22 the side petals are still larger and the first sign appears of the separation of the keel. This process is continued in Figs. 23—25. In Fig. 26 the keel and one of the side petals have become detached from the staminal tube. At this level only the two side sepals remain. Fig. 27 is similar but the other side petal has also become detached. Fig. 28 shows a marked increase in size and an alteration in shape of the keel, a feature connected with the pollination mechanism in *Muraltia*. Fig. 29 passes through the fertile stigma and Fig. 30, slightly higher up, shows a second stigma, in this species possibly non-receptive though stigmatic papillae are produced. In most species of *Muraltia* as in *Polygala*, only the posterior stigma is functional, but here and there, especially in the sub-genus *Psilocladus*, two apparently fertile stigmas are formed. Fig. 31 was drawn from a section passing through two anthers. Unlike *Polygala* the stamens have scarcely any free filaments, the anthers being almost sessile at the end of a staminal tube. The anthers bend upwards, almost at right angles to the staminal tube and as a consequence the anthers appear successively in longitudinal view in transverse sections of a flower bud.

Muraltia esterhuysenae which, as has been pointed out, has several floral features suggestive of *Polygala*, has the floral structure of *Muraltia* with the exception that rudimentary petals are present. An examination of Figs. 32—39 shows this quite clearly. The general appearance of the vascular strands is much like that in *M. flanaganii*, a small difference being that the vascular strands supplying the upper petals separate from the staminal traces at a slightly later stage (Fig. 36). The importance of *Muraltia esterhuysenae* lies in the fact that rudimentary side petals are developed as in *Polygala*. These have no vascular strands and therefore must be regarded as more reduced than those in *Polygala*. Their position, however, shows us that the two lateral stamens which are missing in *Muraltia*, belong to the outer whorl and if present would lie opposite the two anterior sepals. It is therefore possible to construct a floral diagram for *Muraltia*, indicating the positions of the missing stamens (Fig. 40).

MUNDIA.

Mundia spinosa, the only species in the genus, has the same essential floral structure as *Muraltia*. The only noteworthy feature is that the two upper petals make their appearance at the base of the flower before the vascular strands which ultimately supply them have been organised. On taxonomic grounds *Mundia* is best regarded as a specialised off-shoot from the sub-genus *Psilocladus* of *Muraltia*. There is nothing in its floral morphology to oppose this view.



FIGS. 32-39. *Muraltia esterhuysenae*. Sections from the lower part of a flower-bud, showing rudimentary petals (stippled). The shading and symbols are the same as those used in Figs. 1-31.

GENERAL DISCUSSION.

The foregoing account makes it clear that *Muraltia* and *Mundia* are constructed on a different plan from *Polygala*. In *Polygala* one stamen is missing from each of the two whorls. In *Muraltia* the three missing stamens belong to the outer whorl and the inner whorl is complete. In spite of the *Polygala*-like appearance of *Muraltia esterhuysenae*, there can be no doubt that it is a true *Muraltia*. In view of the fundamental difference in floral structure we are able to realise that the flower of *Muraltia* is most unlikely to have eight stamens and the attribution of this number to *Muraltia* in the past must have been founded on faulty observation. Once made, the mistake was perpetuated largely because it had the weight of authority behind it, and also because in dried material the number of anthers is not very easily observed.

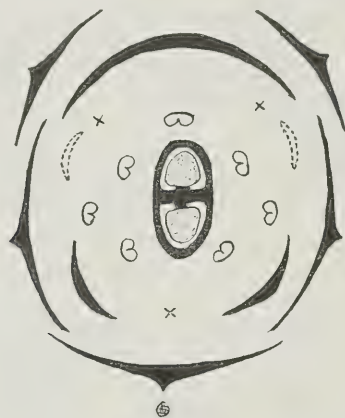


FIG. 40. Floral diagram of *Muraltia*. No attempt is made to show the cohesion and adnation of the various parts. The positions of the missing stamens are indicated by "X." The petals shown with broken lines are present in *M. esterhuysenae* but in none of the other species. In a floral diagram it is customary to show the floral axis at the top of the diagram with the posterior parts of the flower lying immediately next it. In the present case the diagram has been turned through 180° so as to render comparison with the previous diagrams easier.

It is not possible to say which of the two genera, *Polygala* and *Muraltia*, is the more primitive. Both seem to have been derived from some common pentamerous ancestor but evolution has progressed along different lines. The almost complete suppression of the side petals in *Muraltia* suggests that in this respect it has departed further from the ancestral form. On the other hand the occurrence of a few species in

which there are two similar stigmas, both apparently fertile, suggests that *Muraltia* has at times retained a primitive character in the gynoeceum, a character wholly lost in *Polygala*.

It is interesting to note that *Muraltia esterhuysenae*, the most primitive known species of *Muraltia*, occurs on the mountains in the west. Weimarck⁽¹⁴⁾ records the same phenomenon in *Aristea* and it is noteworthy that the only locality known for the primitive *Aristea singularis*, is not very far removed from the locality in which the most primitive species of *Muraltia* has been discovered. A full discussion of the significance of these facts must be postponed until taxonomic work in progress on *Muraltia* is complete.

SUMMARY.

1. In *Polygala* though only three petals develop, two more are present as rudiments. In *Muraltia* rudimentary petals have been seen in only one species. *Mundia* is closely related to *Muraltia* and lacks rudimentary petals.

2. *Polygala* has eight stamens, four belonging to the outer whorl and four to the inner. The missing stamens lie opposite the odd sepal and the odd petal. An exceptional flower with only seven stamens, was observed in *Polygala myrtifolia*. This, however, was due to the disappearance of one of the normal eight stamens and the position of the seven stamens was quite different from those of *Muraltia*. *Muraltia* and *Mundia* always have seven stamens, two in the outer whorl and five in the inner. A stamen is always found opposite the keel.

3. *Polygala* and *Muraltia* have probably evolved along rather different lines from some pentamerous ancestor.

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